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Evidence for interactions among environmental stressors in the Laurentian Great Lakes

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ABSTRACT

Co-occurrence of environmental stressors is ubiquitous in ecosystems, but cumulative effects are difficult to predict for effective indicator development. Individual stressors can amplify (synergies) or lessen (antagonisms) each other's impacts or have fully independent effects (additive). Here we use the Laurentian Great Lakes, where a multitude of stressors have been studied for decades, as a case study for considering insights from both a systematic literature review and an expert elicitation (or structured expert judgment) to identify stressor interactions. In our literature search for pairs of stressors and interaction-related keywords, relatively few studies (9%, or 6/65) supported additive interactions with independent stressor effects. Instead, both antagonisms (42%, or 27/65) and synergies (49%, or 32/65) were common. We found substantial evidence for interactions of invasive dreissenid mussels with nutrient loading and between pairs of invasive species (predominantly dreissenids × round goby), yet both sets of records included mixtures of synergies and antagonisms. Complete quantification of individual and joint effects of stressors was rare, but effect sizes for dreissenid mussels × nutrient loading supported an antagonism. Our expert elicitation included discussion in focus groups and a follow-up survey. This process highlighted the potential for synergies of nutrient loading with dreissenid mussels and climate change as seen from the literature review. The elicitation also identified additional potential interactions less explored in the literature, particularly synergies of nutrient loading with hypoxia and wetland loss. To stimulate future research, we built a conceptual model describing interactions among dreissenid mussels, climate change, and nutrient loading. Our case study illustrates the value of considering results from both elicitations and systematic reviews to overcome data limitations. The simultaneous occurrence of synergies and antagonisms in a single ecosystem underscores the challenge of predicting the cumulative effects of stressors to guide indicator development and other management and restoration decisions.

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1. Introduction

The full suite of anthropogenic stressors impacting an ecosystem can greatly affect the development and performance of indicators for environmental management (Niemi and McDonald, 2004). The effects of individual stressors may not accurately predict changes in the condition of species and ecosystems when stressors co-occur, since multiple stressors can amplify (*synergies*) or lessen (*antagonisms*) cumulative impact. Such interactions among environmental stressors may be common. For example, one broad meta-analysis revealed interactions among stressors in 77% of the experiments examined (Darling and Côté, 2008). Interpretations of past meta-analyses have emphasized the importance of antagonisms over synergies overall (Côté et al., 2016; Darling and Côté, 2008) and for aquatic ecosystems (Jackson et al., 2016). However, identifying the interactions from pairwise studies and integrating those interactions into accurate predictions of stressor effects in real ecosystems can be challenging.

Few ecosystems can be systematically assessed for stressor interactions (e.g., Brennan and Collins, 2015), and harnessing multiple approaches may improve our ability to integrate available information (Mastrandrea et al., 2010; Memon and Thapa, 2011). Factorial experiments, comparative observational studies, and simulation models can be used to produce estimates of the effects of stressors on response variables occurring individually versus together (Côté et al., 2013). Quantitative meta-analyses synthesizing such studies are ideal to evaluate the overall incidence of interactions, but meta-analyses are not reliable with low sample sizes (Rosenberg et al., 2013). In situations where meta-analysis is not feasible, rigorous synthesis can be derived from other forms of evidence synthesis or structured expert judgment (reviewed by Cook et al. (2017) and Martin et al. (2012), respectively). Several forms of data synthesis are available to suit the purpose and question, required level of confidence in output, and available expertise and resources (Cook et al., 2017). One particularly transparent and reliable form of synthesis is a systematic literature review. In systematic reviews, published studies are found and evaluated using explicit criteria to address predefined research questions (Lortie, 2014), allowing an unbiased and replicable survey of the literature for qualitative or quantitative synthesis. A second alternative is expert elicitation (or structured expert judgment), which capitalizes on the broad knowledge and deep abilities of experts to synthesize disparate types of information and to reason through complex relationships (Martin et al., 2012). Many elicitation designs are available to balance different considerations (e.g., respondent bias, group social dynamics, respondent time and effort). Another benefit of expert elicitation in the context of conservation issues is that many designs can be completed rapidly (Martin et al., 2012). As complementary approaches, systematic reviews and expert elicitation together can provide a solid basis for understanding complex environmental problems. Comparing methods may improve data synthesis in policy contexts (Pullin et al., 2016), but even narrative literature reviews and elicitations are rarely formally used together (but see: Memon and Thapa, 2011; Rositano and Ferraro, 2014).

The Laurentian Great Lakes are a globally important system subject to multiple stressors (Allan et al., 2013), and there is a critical need to understand stressor effects, including their interactions. The Lakes are the largest source (18% globally) of surficial freshwater on the planet (Sellinger et al., 2008), support millions of people living and working within the basin, and generate billions (USD) each year economically, particularly in tourism and recreation (Allan et al., 2015; Austin et al., 2007; Vaccaro and Read, 2011). Many anthropogenic stressors co-occur in the basin, including invasive species, climate change effects, urban development, and nonpoint and toxic chemical pollution (Allan et al., 2013). Many ecological indicators for specific stressors and overall condition have been in use (IJC, 2014). The potential for stressor interactions has been identified as a major unmet research need for the Great Lakes (Sterner et al., 2017). Yet, the Great Lakes are reasonably well studied and thus may offer transferable lessons that can be applied to other ecosystems. Expert elicitation has been used successfully to assess current and future stressor impacts in the Great Lakes (Rothlisberger et al., 2010; Smith et al., 2015; Wittmann et al., 2015) but not to assess interactions among stressors.

We expected interactions to be common in the Great Lakes based on the nonlinear changes observed in recent decades, such as food web collapses and algal blooms (Bunnell et al., 2014; Michalak et al., 2013). Bails et al. (2005) hypothesized synergies among various categories of stressors (climate change, nutrient loading, overfishing, toxic chemicals, invasive species, and land use and hydrologic alterations), while others have considered effects of toxic chemicals to be largely additive (e.g., Jackson et al., 2016). Based on previous meta-analyses of interactions (Côté et al., 2016; Crain et al., 2008), we expected antagonisms to be most common. Some stressor combinations have documented mechanistic potential for nonlinear effects, such as invasive mussels moving anthropogenic nutrient inputs from pelagic to benthic food webs (nearshore phosphorus shunt hypothesis: Hecky et al., 2004) and climate change with other stressors promoting regime shifts (Barnosky et al., 2012; Pace et al., 2015).

We paired a systematic literature review and an expert elicitation to explore the incidence of strong and likely stressor interactions in the Laurentian Great Lakes. We aimed to answer the following questions.

- Which pairs of stressors are likely to interact strongly to affect ecosystem condition in the Great Lakes?
- What is the primary direction of each potential interaction (synergy or antagonism)?
- For the pairs of stressors identified as likely to interact based on the elicitation, what is the mechanistic basis of each potential interaction?

Although we found the availability of empirical data on stressor interactions for the Great Lakes to be limited, the systematic review and expert elicitation together allowed us to summarize current evidence, identify potential effects, and highlight the importance of further study of stressor interactions to better understand ecological impacts.

2. Methods

Interactions (synergies and antagonisms) have been defined in several ways (Folt et al., 1999; Piggott et al., 2015). We used additive thresholds, whereby the joint effect of two stressors without an interaction is the sum of the two individual stressor effects, hereafter considered an *additive* interaction type (Fig. 1). A *synergy* between two stressors is defined as a case where the two stressors together have a joint effect greater than the sum of the individual effects, and an *antagonism* is defined with a joint effect less than the sum of the individual effects of the two stressors (Folt et al., 1999; Fig. 1).

We framed our study on a set of 50 environmental stressors across eight categories collated by the Great Lakes Environmental Assessment and Mapping project (GLEAM; Smith et al., 2015). We limited the current study to pairwise combinations of select stressors, since higher-order interactions are even less understood (Billick and Case, 1994). However, we noted cases where additional factors affected pairwise interactions. We designed our study to highlight interactions that were both likely and potentially strong, rather than attempting to exhaustively document all possible pairwise combinations.

2.1. Literature review

We used a literature review to assess current data for the occurrence of interactions in the Great Lakes. The literature search (conducted January 2014 - June 2015) was structured as both a Cochrane-style systematic review and as a meta-analysis (Côté and Jennions, 2013; Curtis et al., 2013; Higgins and Green, 2011). We primarily identified studies using keyword strings with two target stressors and “Great

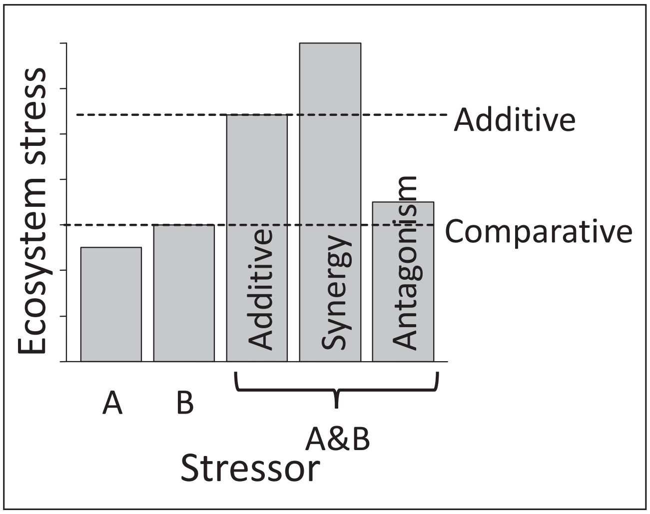

Fig. 1. Conceptualization of interactions between environmental stressors. We assume two stressors ("A" and "B") each have individual effects on ecosystem condition measured by a relevant response variable (left two bars). The joint effect ("A & B") of the two stressors together is defined as additive when the combined effect is approximately equal to the sum of the two individual effects ("additive" bar and dotted line), synergistic when the joint effect is greater than the sum ("synergy" bar), and antagonistic when the joint effect is less than the sum ("antagonism" bar). Others have used alternative definitions of interactions (e.g., "comparative" dotted line, equal to the larger individual stressor effect). Measurement units here are arbitrary.

Lakes" or any of the five individual lakes. We searched for all pairwise combinations of eight stressors that were highly rated individually in a prior survey (Smith et al., 2015) as well as for additional pairs of stressors potentially representing secondary effects of other stressors, such as harmful algal blooms and changes in native fish populations (Appendix Table A.1). We used the Web of Science Core Collection (ISI Web of Knowledge), excluding conference proceedings and reports. In addition to these searches, we evaluated additional studies opportunistically (e.g., nominated by our team of authors or cited by included studies), resulting in five additional studies in the qualitative synthesis.

We filtered studies hierarchically to identify empirical data on both individual and joint effects. Criteria for inclusion were presenting primary data from original research (i.e., experiments, models, or field surveys - not a review), including multiple stressors and an interaction, presenting data on relevant response variables (e.g., ecological effects rather than human effects of pollutants), and applying to lakes. (Most studies applied to lakes based on our search terms, but a few studies from other ecosystem types needed to be excluded due to Web of Science's "keywords plus" database field). Most studies were excluded during initial screening based on title and abstract, but additional studies from broader searches were excluded based on title only (Appendix Table A.1) or after reading the full text. In the screening process, we added some studies that were originally excluded to increase our sample size for the qualitative synthesis (Fig. 2).

We designed the review to estimate effect sizes using meta-analysis but also extracted qualitative conclusions from the studies. Multiple datasets (hereafter *records*; note transition from *studies* in Fig. 2) were extracted from a single study when data from multiple pairs of stressors were presented (e.g., 3-way factorial experiments could cover three pairs of stressors). For data extraction, we focused on one response variable relevant to ecosystem condition in each study. While most meta-analyses include all response variables from a study as separate records, we chose just one variable representative of all variables presented to avoid undue influence of any one study (e.g., one mesocosm experiment may have multiple correlated response variables). Given this choice, we excluded two studies in which the overall joint effect was unclear (both studies had multiple relevant response variables contradicting each other).

For meta-analysis, we extracted estimates (means and standard deviations) of the control effect, the individual effects of each stressor alone, and the joint effect of both stressors together from the text or tables of the results or by digitizing figures. We $\log_{10}$-transformed the raw magnitudes when needed so that all response variables were on similar scales, but did not convert the data to percentages. Sample sizes of at least five studies are recommended for formal meta-analysis of an effect size (Rosenberg et al., 2013). Thus, we were able to calculate effect sizes only for the most commonly studied interaction of invasive mussels × nutrient loading. For this stressor pair, we calculated Hedges' *d* using the escalc function from the metafor package (version 1.9-4) in R 3.0.1 ("SMDH" measure option; R Core Team, 2013; Viechtbauer, 2010). Hedges' *d* is a commonly used effect size metric for the standardized difference in means that is robust to heteroskedasticity in sample variances (Bonett, 2008; Hedges and Olkin, 1985; Rosenberg et al., 2013).

To assess interactions for stressor pairs beyond invasive mussels × nutrient loading, we also qualitatively summarized available records. We classified results as additive, synergistic, or antagonistic based on the definitions used here, which sometimes conflicted with stated conclusions due to alternative definitions of interactions (Fig. 1). For example, some studies used a comparative definition, where the threshold is the larger of the two individual stressor effect (Folt et al., 1999; Fig. 1), but we prefer the additive thresholds for simplicity of interpretation. We tallied counts of interaction types, evaluating by stressors, response variables, and potential covariates (location, methodology, year of manuscript publication).

2.2. Expert elicitation

Expert elicitation (or structured expert judgment) provided an ideal complementary approach to identify interactions given the limited study of stressor interactions and their mechanistic complexity. Experts were selected based on depth and breadth of topical expertise across eight categories of stressors, also aiming for a diverse team in work sector, career stage, and gender to promote high-performing collaboration (Cheruvelil et al., 2014).

Experts were instructed to identify interactions that were likely and potentially strong in the Great Lakes and to predict the direction of the interaction and the mechanisms involved. The elicitation was not designed to identify weak interactions or additive effects. After discussing the definition of interactions and goals together, four focus groups of 3–4 people crossed the stressors from two of the eight stressor categories (9–16 stressors total; each group had a different subset of stressors) with all 50 individual stressors from the GLEAM Project (Appendix B). Each focus group filled out a tabular recording sheet marking synergies and antagonisms that were likely and potentially strong, specifying the individual stressors involved (Appendix B), and we also recorded the conversations (but the recording failed for one group). After completing all stressor crosses (in 80 min for most groups), the groups identified 2–5 particularly likely and potentially strong interactions for further assessment. From this process, 16 interactions were identified and summarized as a large group.

A follow-up questionnaire was designed to cover each of the 16 proposed key interactions, specifying the type of interaction (synergy/antagonism) and putative mechanisms (Appendix B). The questionnaire was distributed via email, and experts independently voted for the five most likely and strong interactions from the set of 16. Selections were tallied to gauge experts' opinions of the relative importance and support for each interaction.

We also compared these results to the literature review, since the agreement of multiple lines of evidence can increase scientific confidence (Mastrandrea et al., 2010; Memon and Thapa, 2011). When results from the two methods did not agree, we considered this to be

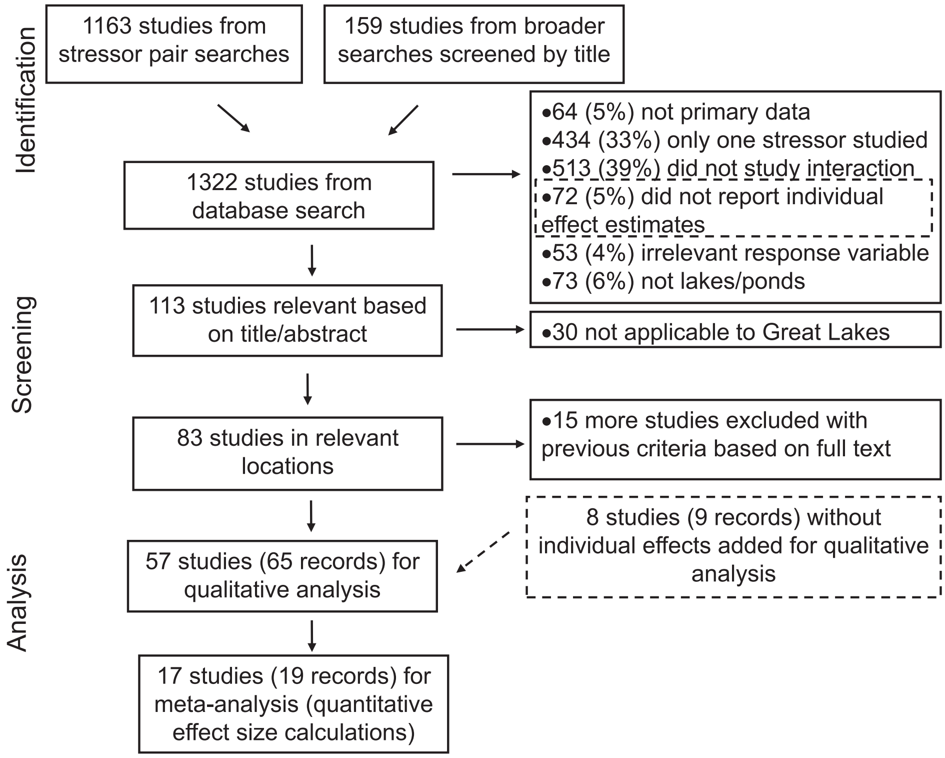

Fig. 2. Search process for the systematic review of interactions between environmental stressors in the Laurentian Great Lakes. Flowchart (modified from Moher et al., 2009) indicates steps of the systematic literature review from identifying studies and screening for relevance to extracting data for analysis. “Studies” are considered published articles and “records” are datasets within articles. Boxes to the right denote studies excluded; screening criteria are listed in the order evaluated with percentages and counts. Boxes with dotted outlines indicate studies that were originally excluded based on screening for estimates of the individual effects needed for meta-analysis. These 72 studies were reevaluated for the qualitative synthesis through the same further screening (relevant response variable, applicable to lakes/ponds generally and the Great Lakes specifically, and conducted in relevant locations), and eight studies satisfying those criteria were added to the qualitative synthesis. The shown initial search hit counts include duplicates.

indicative of the complexity of stressor interactions, and we critically evaluated contrasting evidence for potential interactions on a case-by-case basis. In some cases, we felt that the two methods captured different types of effects at different scales, since the systematic review (particularly for experimental data) gave more concrete evidence but had weaker ability to detect large-scale changes and processes.

2.3. Conceptual modeling

To better understand the mechanistic basis for stressor interactions, the working group developed conceptual models for several pairs or triplets of stressors. This exercise was partly informed by the prior expert elicitation and combined knowledge of relevant literature, but can be considered a third approach to understanding synergies based on a conceptualization of interacting processes. Only one example (which combined two of those original models; see 4. Discussion) is included here to spur research and illustrate the complexity resulting from multiple, interacting mechanistic pathways. It certainly under-represents the true complexity of the ecosystem.

3. Results

In the literature review, 65 records were extracted from 57 studies with qualitative information about the single and joint effects of stressors in the Great Lakes (Fig. 2). Of the 1322 original search hits, most studies were excluded due to missing data for one stressor or the joint effect (Fig. 2). From the stressor searches, studies dealing with pairs of stressors related to invasive species (68%), climate change (30%), and nutrient loading (30%) were most common; studies of toxic chemicals (20%) and coastal development or habitat alterations (15%) were less common (n = 1175 studies). We attempted to extract raw data from 113 studies (8.5% of original search hits), but only 19 records from 17 studies had complete quantitative data (< 2% of all studies) (Fig. 2).

Synergies (49%) and antagonisms (42%) were most common among the qualitative data records, and relatively few studies (9%) were recorded as additive (n = 65 records; Fig. 3A). Some response variables primarily had one interaction type, such as native invertebrates (the number, density, mortality, or biomass of non-dreissenid invertebrates) often showing antagonisms, and nutrients (usually phosphorus levels or movement) often showing synergies. However, most response variables were inconsistent in interaction type (Fig. 3B). By study type, observational studies more often trended toward synergies, experiments more often trended toward antagonisms, and mathematical models were mixed in interaction types (Fig. 3C).

The most records addressed interactions of invasive species × nutrient loading (predominantly dreissenid mussels × phosphorus) and interactions between pairs of invasive species (predominantly dreissenid mussels × round gobies), and both sets of records had mixes of synergies and antagonisms (Fig. 3A). For the variability of interaction types for invasive species pairs, the variability was partly associated with response variable: most antagonisms were for responses of invertebrate communities (6/8 records), and most synergies were for responses of toxic chemicals (2/5) and native vertebrates (2/5). However, sample sizes for studies quantitatively estimating both single and joint effects were insufficient to calculate Hedges’ *d* effect sizes for the invasive species pairs.

For invasive species × nutrients, the mix of interaction types was

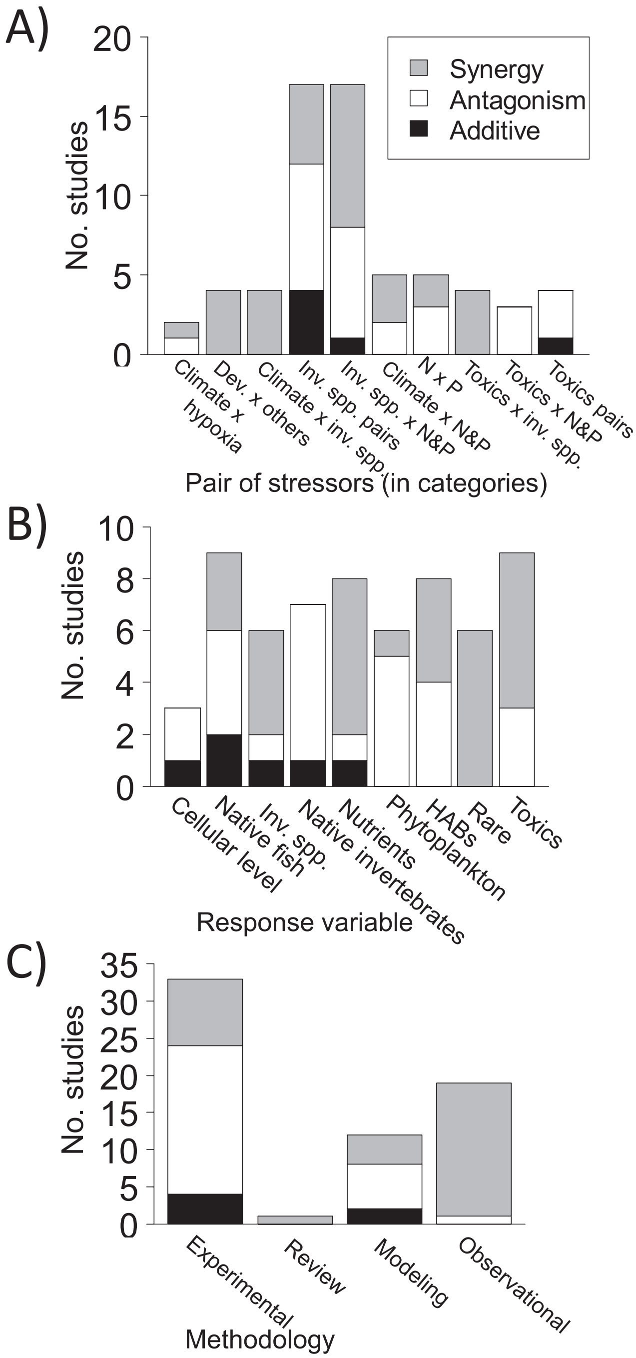

Fig. 3. Frequencies of interactions of environmental stressors in the Laurentian Great Lakes based on the systematic review. Interaction types (synergistic, antagonistic, or additive, separated by color) are shown by stressor pairs (A), by response variables (B), and by study methodology (C). The types were determined qualitatively (n = 65 records from 57 studies). Stressors in (A) are grouped into larger categories, and coastal urban development ("dev.") is shown paired with all other stressors. For response variables in (B), native invertebrates are non-dreissenid invertebrates, and cellular level responses include cancer proliferation and erythrocyte activity. Rare responses in (B) are shown together; they included botulism, *Cladophora*, and emergent vegetation. [Other abbreviations: Inv. spp. = invasive species; N × P = nitrogen loading × phosphorus loading; climate = climate change; HABs = harmful algal blooms].

associated weakly with study type and publication year. Most of the synergies were for earlier (mostly 2004–2011) publications, while most of the antagonisms were for later (mostly 2012–2015) publications. The observational studies in this set of records were all synergies, whereas experimental and modeling studies had mixes of synergies and antagonisms. Based on the quantitative data for invasive mussels × phosphorus loading, Hedges' *d* effect sizes for the standardized difference between means of each treatment versus the control supported categorizing this interaction as antagonistic (mean ± 1 SE for dreissenid mussel individual effect: 0.73 ± 0.34, nutrient individual effect: 0.93 ± 0.36, joint effect: 1.10 ± 0.37, vs. an additive effect would have been ~1.66; n = 6 records). Response variables for most (5/6) of these records were phytoplankton-related.

In the qualitative analysis of pairs of stressor categories with fewer records, climate change × invasive species, toxics × invasive species, and coastal development paired with different stressors had the most qualitative evidence for synergies (n = 4 records each), while toxics × nutrient loading and pairs of toxics had the most evidence for antagonisms (n = 3 and 4 records each; Fig. 3A). Climate × nutrient loading and pairs of two nutrients (all N × P) were mixed (Fig. 3A).

In the elicitation, experts identified multiple likely and potentially strong synergies and a few antagonisms (Table 1, Appendix Table A.2). Respondents particularly highlighted that nutrient loading can interact synergistically with other stressors, including climate change, coastal development, invasive mussels, and hypoxia. Mechanisms for these interactions included increasing the quantity of nutrients via feedbacks with other stressors and nutrients fueling nuisance algae and plant growth. Coastal development also appeared in multiple moderately-ranked interactions, such as with nutrient loading (synergy), water level changes due to climate change (either direction), and invasive round gobies (synergy). Mechanisms included altered nutrient cycling and wetland loss or gain modifying critical habitat for associated organisms. Respondents also identified the quantity of sediment as a feedback promoting an antagonism for tributary dams × sediment loading, and increased productivity promoting a synergy for climate change × hypoxia.

Comparing the literature and elicitation results, we found that nutrient loading × invasive mussels and nutrient loading × climate change had support from both methods as potential interactions, although the literature suggested variability in interaction type while experts predicted synergies (Fig. 4). Other interactions were highlighted by only one method. For example, interactions between toxic chemicals were not emphasized in the elicitation, but literature suggested that some pairs of chemicals can interact antagonistically.

4. Discussion

We identified several likely and potentially strong interactions among environmental stressors in our case study of the Laurentian Great Lakes. Our systematic review suggested that synergies may be common and additive effects may be rarer than expected in the Laurentian Great Lakes, but several of the supported interactions were inconsistent in direction (synergy vs. antagonism). Our elicitation added support for some synergies in the Great Lakes. Overall, our systematic review and meta-analysis allowed for focused assessment of research to date, while our expert elicitation allowed inclusion of less studied stressors and provided deeper insight into mechanisms underlying interactions.

Both the systematic review and expert elicitation highlighted interactions among nutrients, invasive mussels, and climate change. A focus on interactions among these stressors (e.g., rather than other highly rated invasive species: Smith et al., 2015) made sense given their potential for changing bottom-up processes, food web structure, and abiotic drivers, respectively (Barnosky et al., 2012; Bunnell et al., 2014; Pace et al., 2015). These interactions fit with current concerns in the Laurentian Great Lakes as well (e.g., harmful algal blooms: Michalak et al., 2013). To stimulate future research, we present a conceptual model synthesizing the relationships among some mechanisms graphically that we built after the elicitation (Fig. 5). We suggest that increased runoff (top arrow in Fig. 5) associated with climate change may

Table 1
Likely and potentially strong interactions between environmental stressors in the Laurentian Great Lakes based on expert elicitation. Shown are the pair of environmental stressors, the number of respondents (out of 12) selecting the stressor pair in their top 5, and a brief description of major mechanism(s). Interactions with > 20% of respondents indicating top 5 importance shown here; see Appendix Table A.2 for all interactions selected by the focus groups.

Stressor pair	No.	Interaction type and mechanisms
Nutrient loading × climate change impacts	10	Synergy: Nutrient loading will increase with flashier/higher river discharge, and stressors together favor nuisance algal blooms and accelerated cycling
Nutrient loading × coastal development	9	Synergy: Loss of wetlands exacerbates negative effects of nutrient loading due to reduced nutrient trapping and removal
Nutrient loading × invasive mussels	9	Synergy: Nearshore shunt traps nutrients nearshore and decreases them offshore; stressors together enhance nuisance blooms (e.g., HABs, *Cladophora*) and nearshore aquatic plants
Nutrient loading × hypoxia	7	Synergy: Phosphate is released from the sediment into the water column under hypoxic conditions
Climate warming water temperature × hypoxia	6	Synergy: Warmer waters will fuel longer stratification and higher algal productivity, leading to greater area and longer lasting periods of hypoxia
Tributary dams × sediment loading	4	Antagonism: Dams attenuate sediments, further reducing effects on lakes
Coastal development × changing water levels due to climate change	3	Antagonism or synergy: Lower water level moves the shoreline away from development, allowing for wetlands to recover/develop between the water and the hardened shoreline, and v.v
Coastal development × round goby	3	Synergy: Loss of native fish spawning habitat; wetland habitat where native fish thrive (but gobies do not) is removed and replaced with ideal goby habitat (e.g., riprap)

increase nutrient loading (Bosch et al., 2014; Culbertson et al., 2016; Robertson et al., 2016; Rowe et al., 2017) and bioavailability (Maccoux et al., 2016). Also, mussels may promote benthification (creating particulate matter, locking nutrients within benthic food webs and impeding transfer to offshore pelagic food webs: Bunnell et al., 2014; Hecky et al., 2004; Rowe et al., 2017 – "nearshore retention, nutrient excretion" arrow in Fig. 5 represents these novel food web shifts). Additionally, many individual pathways for primary production and recycling within the ecosystem can create positive feedbacks that amplify each other (Fahnenstiel et al., 2010; Hecky et al., 2004). Indirectly these stressors may promote shifts in producer community composition to harmful and nuisance algal blooms (Fahnenstiel et al., 2010; Hecky et al., 2004).

Even this simplified view of possible mechanisms suggests complex relationships difficult to capture in a causal diagram that accurately represents contributing factors and current uncertainties. While we attempted to document only pairwise interactions between stressors in the review and elicitation, higher-order interactions are likely (Billick and Case, 1994; also see Fig. 5), and current work is beginning to explore them (Rowe et al., 2017). Our data collection in the literature review supported the potential for multi-way interactions, since 48% (27/56) of the qualitative records explicitly discussed covariates (a third stressor or factor affecting the relationship between the two stressors studied). For example, from an observational study of the invasive plant *Myriophyllum spicatum* (Ginn, 2011), we extracted data for the invasive plants × phosphorus loading, but dreissenid mussels were discussed as contributing to the changes observed.

We succeeded in identifying several likely and potentially strong synergies and antagonisms with support from both the expert elicitation and the systematic review, but these two approaches also yielded intriguing contrasts. The expert elicitation results particularly emphasized synergies between nutrient loading and other stressors, whereas the literature review revealed a diverse mix of synergies and antagonisms most often involving invasive species. The experts' emphasis on nutrients did not seem to be a result from respondent bias (e.g., only 4 of 13 participants have focused their research on nutrients or primary producers) or recent publication trends (e.g., more recent invasive mussel × phosphorus loading studies trended toward antagonisms).

Stressor pair	Elicitation findings	No. (lit.)	Systematic lit. review findings		
Nutrient loading x invasive mussels	Synergy	14	50% Synergy	50% Ant.	
Climate change impacts x nutrient loading	Synergy	5	60% Synergy	40% Ant.	
Invasive mussels x invasive fish	N/A	13	23% Syn.	31% Add.	46% Ant.
Toxic organics x nutrient loading	N/A	3	100% Antagonism		
Toxics with each other	N/A	4	25% Add.	75% Antagonism	
Coastal dev. x nutrient loading	Synergy	1	100% Synergy		
Climate warming water temperature x hypoxia	Synergy	2	50% Syn.	50% Ant.	

Fig. 4. Comparison of systematic review and expert elicitation results for likely and potentially strong interactions between environmental stressors in the Laurentian Great Lakes. Shown are the pair of stressors, the interaction type based on the elicitation, the number of records for qualitative synthesis from the systematic review, and the proportion of records for each interaction type in the literature records separated by color (grey for synergies, black for additive effects, and white for antagonisms). "N/A" indicates no or minimal data.

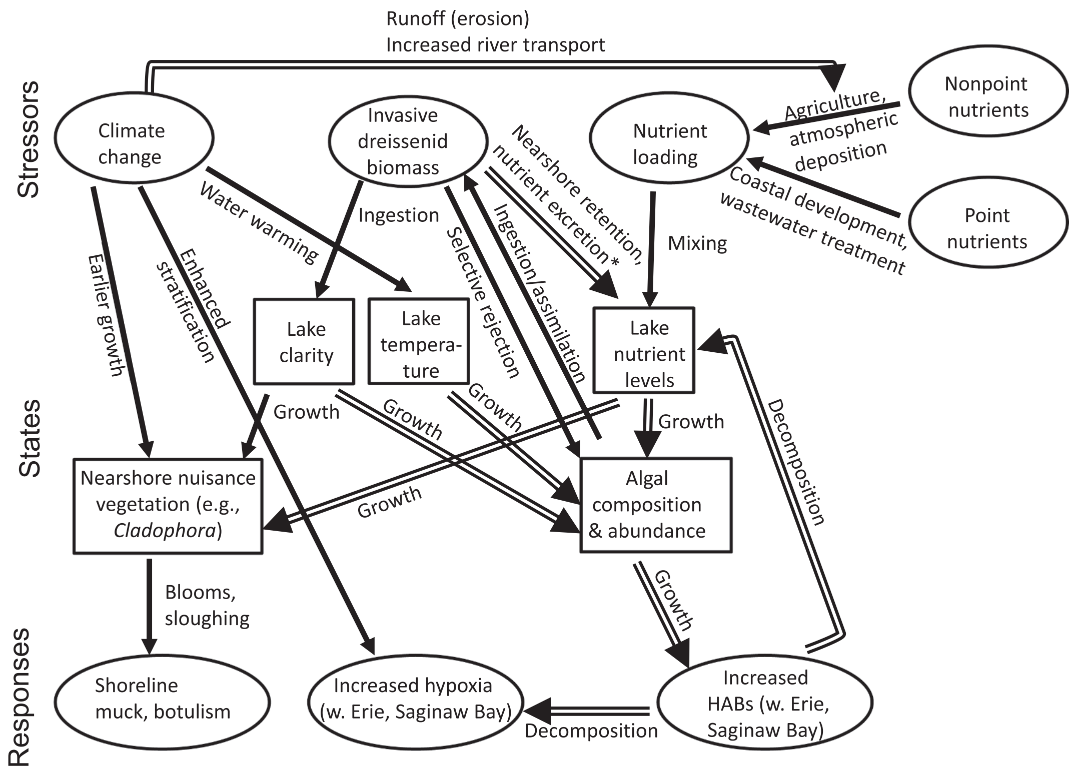

Fig. 5. Conceptual model of example interactions in the Laurentian Great Lakes based on expert working group discussions. We integrate some of the interactions predicted between climate change, nutrient loading, and invasive dreissenid mussels with potential mechanisms behind these interactions. Stressors and contributors (smaller ovals) are shown affecting variables reflecting ecosystem state (rectangles) to produce ecosystem responses of management concern (larger ovals). Note that hypoxia and harmful algal blooms (HABs) are issues primarily restricted to particular geographic locations within the Great Lakes. Labeled arrows represent processes, contributing stressors, and mechanisms; double-lined arrows represent processes which may occur and/or be amplified due to potential stressor interactions. (From these potential interactions, we considered the asterisked process a novel food web shift but the others to be primarily amplifications.)

Rather, the emphasis on invasive species in publications may result from investigators considering invasive species particularly important in the Laurentian Great Lakes, other stressors being hard to study (feasibility), and/or studies of other stressors being harder to fund (bias in funding opportunities).

For the best-studied interaction of dreissenid mussels × nutrient loading, evidence for the interaction type was inconclusive. Our quantitative data supported an antagonism, previous hypotheses (Bails et al., 2005; Hecky et al., 2004) and our elicitation supported a synergy, and the qualitative literature analysis supported variability in effects. One explanation for these different conclusions is that effects can differ by location, context, and timing. For example, hypoxia may be a major synergistic consequence of this interaction in Saginaw Bay and central Lake Erie, but hypoxia does not affect the deeper waters of eastern Lake Erie and the other lakes (Hawley et al., 2006; Siersma et al., 2014; Zhou et al., 2012), allowing antagonistic consequences to dominate. Another possibility is scaling issues with mesocosm experiments. Some of the mechanisms discussed in the context of synergies, such as the nearshore phosphorus shunt, may not operate in mesocosm experiments within small lakes, but rather are inherently large-lake phenomena or develop on longer time scales. Finally, published quantitative studies often dealt with subsets of the mechanisms and species in the lakes. For example, Sarnelle et al. (2012) suggested mechanisms involving the balance of nutrient recycling and grazing rates, but these are just two of several potential processes and feedbacks in our conceptual model (Fig. 5). Similarly, Sinclair and Arnott (2015) focused primarily on zooplankton, whereas we and others have highlighted endpoints in phytoplankton composition and hypoxia (Fig. 5). While future factorial mesocosm experiments will help to explore potential interactions further, the published mathematical models from our review also allowed the study of interactions with supportable assumptions and may be a feasible alternative to bridge scales.

Compared to the broader sets of ecosystems included in past syntheses, more synergies were found in the Laurentian Great Lakes literature (49% here vs. 28–36% range among meta-analyses by Crain et al. (2008), Darling and Côté (2008), and Jackson et al. (2016)). This trend partly may be due to having fewer factorial experiments in our study, since modeling and observational studies in our synthesis were more often synergistic. However, this trend was supported by the expert elicitation results emphasizing synergies. Further, an almost-even mixture of synergies and antagonisms (49% synergy vs. 42% antagonism in our study) was consistent with the findings of others [e.g., differences in percentages between synergies and antagonisms of 2% (36% vs. 38%) in Crain et al., 2008; 7% (35% vs. 42%) in Darling and Côté, 2008]. Thus, recognizing a diversity of interactions within the Laurentian Great Lakes and in other systems may be warranted. The strongest difference from past meta-analyses is our lack of additive effects. Our elicitation was not designed to measure these effects given its emphasis on synthesizing knowledge of particularly likely and strong interactions, but our systematic review did. The review suggested fewer additive effects in the Great Lakes than seen in broad meta-analyses (9% here vs. 26% in Crain et al. 2008, 23% in Darling and Côté, 2008), although the meta-analysis of aquatic ecosystems by Jackson et al. (2016) had more similar results with 16% of studies having additive effects. While a lack of additive effects may be attributable to publication bias (Jennions et al., 2013), we may have had less chance to detect additive effects with the low sample size in our qualitative vote-counting.

Interactions among stressors can have important consequences for ecosystem monitoring and management. For ecological indicators that are developed to gauge specific stressors, indicators need to have predictable and sensitive responses to the stressors of interest that are not

obscured by other factors (Niemi and McDonald, 2004; Siddig et al., 2016). Thus, additional stressors interacting with the stressors of interest may make indicators of specific stressors less robust. Similarly, for indices of cumulative human impacts (e.g., Halpern et al., 2008 model applied to the Laurentian Great Lakes in Allan et al., 2013), stressor interactions may lead to dramatic over- and underestimates of total stress. For example, Brown et al. (2013) found that adding one antagonism into a two-stressor model caused alleviating one stressor to deteriorate overall ecosystem condition in some cases. Our findings suggest that incorporating both synergies and antagonisms into management tools may be necessary. Yet, even as science is pushed toward the better prediction of interactive effects, we may never be able to predict all of the binary and higher-order interactions (Billick and Case, 1994), particularly for the dozens of co-occurring stressors seen in this ecosystem (Allan et al., 2013). Thus, having an inclusive view of interactions that allows for additivity, synergies, and antagonisms, as well as directing both indicator development and management actions to choices safe under multiple scenarios (Côté et al., 2016; Gunderson, 2000), may be the most practical approach.

Data availability on the strength and direction of interactions is limited in many ecosystems of conservation concern. Many methods of synthesis are available but have tradeoffs in resources and time needed, level of certainty, rigor, transparency, updateability, and repeatability (Cook et al., 2017; Pullin et al., 2016). Using more than one method in parallel to synthesize information and opinion counterbalances the pros and cons of individual methods and adds to overall confidence (Mastrandrea et al., 2010; Memon and Thapa, 2011; Pullin et al., 2016). Meta-analyses are ideal to evaluate evidence when many datasets are available. However, for indicator development and management decisions in ecosystems with limited data availability, our approach of considering insights gained from expert judgment and alternative forms of synthesis may be useful.

5. Conclusions and future directions

Studies of interactions among co-occurring stressors were surprisingly few in the Laurentian Great Lakes, highlighting a need for more studies with explicit measurements of both individual and joint effects of stressors. Simulation models may help to study the incidence of stressor interactions at larger scales than can be manipulated in factorial experiments. Evidence from our literature review, as visualized in our conceptual model, highlighted that multi-way interactions and complex mechanisms may add uncertainty to predictions of ecosystem impacts. Thus, in the absence of stressor-specific information to tailor actions, on-the-ground management may need to be directed toward strategies that effectively incorporate multiple stressor interaction types (additivity, synergies, and antagonisms) and increase overall ecosystem resilience.

6. Declarations of interest

None.

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Appendices A and B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.01.010.

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